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Spatial distribution of arthropods along the seashore catena of the Kunashir island (the Kurils)

Пространственное распределение членистонгих вдоль катены на морском побережье Курильского острова Кунашир

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KEY WORDS: Arthropods, catena, seashore, succession, population density, Kunashir island.

КЛЮЧЕВЫЕ СЛОВА: членистногие, катена, берег моря, сукцессия, население, остров Кунашир.

ABSTRACT. Distribution of arthropods of 80 species was studied along the catena slope from ocean to the shore rocks. Total abundance of arthropods decreases geometrically with the distance from the water edge whereas their diversity increases 3–fold. All species were divided into 5 ecological groups based on their preference to geomorphologic positions of catena: a) amphibionts preferring water margin; b) hygrophilic beach species; c) mesophilic species of the steep cliff slope; d) meadow oligophilic species of the abrasion plane, and e) forest oligophilic species of the piedmont plain. Irrespective of their phylogenetic position, the species of each group generally display similar patterns of life strategy. Each catenary position is characterised by specific combination of ecological groups, with one of them dominating in species diversity and numbers. This spatial sequence of arthropod communities may be regarded as succession with amphibionts representing the initial, and beach hygrophiles, mesophiles, meadow and forest oligophiles — further stages of succession, up to the climax one. Quantitative domination of a certain ecological group in a community indicates the stage of succession. According to the hypothesis of Pickett et al. [1987], a succession might be directed by one of the following models: stimulation, toleration and inhibition. All the three mechanisms functions simultaneously at different positions of the catena, and successively in its central part.

РЕЗЮМЕ. На острове Кунашир Курильского архипелага проанализировано количественное распределение 80 членистоногих животных в градиенте экологических условий — от уреза океана до коренного берега. В этом направлении обилие населения снижается в геометрической прогрессии, разнообразие видов увеличивается втрое. По количественному предпочтению геоморфологических позиций катены выделено 5 экологических групп видов: амфибионты, предпочитающие урез воды; гигрофилы пляжа, мезофилы крутого волноприбойного откоса, луговые олигофиты абразионного уступа и лесные олигофилы предгорной равнины. Независимо от филогенетических отношений, виды одной экогруппы имеют сходный тип жизненной стратегии. На каждой геоморфологической позиции катены складывается особая композиция экологических групп с доминированием видов и особей одной из них. Этот ряд сообществ членистоногих можно рассматривать также и как сукцессионную серию. Виды-амфибионты маркируют инициальную, пляжные гигрофилы, мезофилы, луговые и лесные олигофилы — последующие стадии сукцессии, вплоть до климаксовой. Количественное доминирование той или иной экологической группы в сообществе указывает стадию развития сообщества в момент учета. Широко распространено мнение [Pickett et al., 1987], что сукцессии происходят следуя избирательно одной из известных моделей: стимуляции, толерантности, или ингибирования. На изученной приморской катене все три модели развития сообщества проявляются одновременно, но на разных позициях катены, и последовательно на ее срединной позиции.

Introduction

There are several reasons for the high interest of researchers to animal population of tidal areas.

First, environment and communities of tidal zones have maintained constant outlook and structure for hundreds of millions of years and thus may be regarded as a perfect reference of of conservatism in nature.

Second, the tidal zone is a very complicated ecotone where three different media (water, air and soil) are interfacing. In such a marginal habitat selection favours organisms with non-specific adaptations to rapid, frequent and drastic environmental changes. Such

organisms have a high potential for further evolution [Mamkaev, 1968; Berezina, Mordkovich, 2000]. Therefore such ecosystems are often regarded as a cradle for at least terrestrial insects [Ghilarov, 1970; Ponomarenko, Zherikhin, 1980; Tshernyshev, 1996].

Third, sea beaches represent an area of classic successions. The latter occur there in regular cycles from month to month, year to year, century to century. The stages of such cycles are so distinctly differentiated in time and space as nowhere else on Earth. Such distinctness is guaranteed by regular tide flows governed from cosmos.

Though publications about water invertebrates on sea beaches are quite abundant, studies concerning terrestrial animals are relatively scarce [Anderssen, 1985; Evans, 1977; King et al., 1982; Topp, 1979]. Meanwhile, both these components of beach animal population form one single whole. So the aim of this study was i) to characterise quantitative distribution of water- and land-dwelling animals along the ecological gradient from water edge to piedmont, and ii) to explain the pattern of taxa substitution in beach catena communities.

Materials and Methods

Characteristics of the study site

The seashore represents a catena of 350 m long, consisting of the chain of ecosystems (Fig. 1). The catena has 5 distinctly distinguishable positions:

1) Water margin, 15–20 m wide, with ebb/flood frequency of 6 hours (tidal cycle). Numerous seaweed ridges deposited by tidal flow are 5–15 cm wide and 5–8 m long and stretch along the seashore line, alternating each 3–5 m with stripes of bare sand. Due to frequent moistening by cold sea water (5–8 °C), sand temperature at the depth of 5 cm does not exceed 18°C even in the warmest time of the day. There are no higher plants.

2) Beach, *ca.* 20 m wide and flooded by high tides twice a month. Stripes of bare sand alternate with organic residues, consisting not only of seaweed, but also of tree branches, bark and anthropogenic waste. deposited by waves. Midday sand temperature may reach 28–30°C at the depth of 5 cm, and 47–52°C on the surface, depending on sand colour and moisture content. Higher vegetation is represented by scarce psammophytes (*Elymus, Artemisia* etc). Occasionally tree trunks or pieces of wood brought by strong storms are present. Such trunks provide microsites of very moderate environmental conditions.

3) Cliff, a steep (40–45°) slope with a dense vegetation of dogroses, wild grapes and diverse meadow herbs (*Pelargonia, Fabales, Tris, Apiaceae* and others). A short profile of well structured soil rich in humus is characteristic for the site. Waves reach the cliff only during the strongest storms.

4) Abrasion plane, above the cliff, composed by a huge layer of sediments over the crystalline basement. The terrace is *ca.* 50 m above the beach and is occupied by meadow vegetation similar to the one of the cliff, but with scarce bamboo plants (*Sasa* sp.). The wind from the sea brings occasional spatter. Gradually the terrace changes into piedmont.

5) *Piedmont*, the plain elevated by tectonic processes, stretches above the abrasion plane up to 800 m above sea level. It is mainly covered by subtropic deciduous forest (*Quercus, Acer, Magnolia, Carapalax* etc.) The areas above are covered by coniferous fir-and-spruce forests, being out of this study scope.

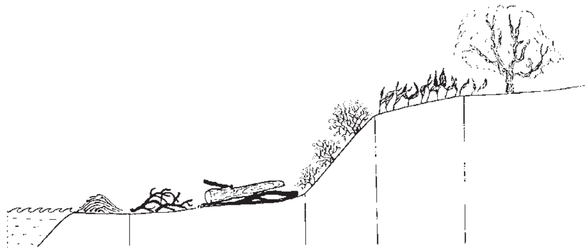


Fig. 1. The seashore catena on the Kunashir island of the Kuril archipelago, geomorphologic positions: water margin (1), beach (2), cliff (3), abrasion plane (4), piedmont (5).

Рис. 1. Береговая катена острова кунашир Курильского архипелага, геоморфологические позиции: урез воды (1), пляж (2), клиф (3), абразионная терраса (4), пьедмонт (5).

Methods to determine the numbers of arthropods

Herpetobiotic arthropods were collected in summer 1992 on the southern shore of Kunashir island, Kuril Archipelago (Fig. 1). The island has mostly forest landscape with subtropical deciduous or boreal fir-spruce forests.

Diversity and activity of arthropods were estimated by means of Barber's pitfall traps. Plastic glasses (66 mm in diameter) were used as traps. Twenty traps were distributed at random in 5 rows in each biotope. Three successive samplings were carried out, each after 5 days of trap exposition. The dynamic population density was expressed per 1 m^2 of the trap area per day.

To compare communities the following index of difference was used:

$$\rho = \sum_{k=1} \alpha_k^1 - \alpha_k^2 \sqrt{(\sum_{k=1}^{n} \alpha_k^1 + \sum_{k=1}^{n} \alpha_k^1)}\ ,$$

where α_k^1 and α_k^2 are numbers of a certain species (k) in the 1st and 2nd communities, respectively, while $\sum \alpha_k^1$ and $\sum \alpha_k^2$ are the sums of species numbers from 1 to n species of the 1st and 2nd communities, respectively.

The index of biological diversity was also used to compare communities: $M = \frac{a}{\sqrt{b}}$,

where *a* stands for the total number of species, and *b* is the total number of animals in a community [Magarran, 1992].

Results

General abundance

Overall, 80 species of arthropods were found in the tidal zone of Ivanovsky foreland of the Kunashir island. Those species represent just a small part of the island fauna [Krivolutskaya, 1973; Kryzhanovsky et al., 1975]. The arthropod fauna included representatives of 3 subtypes: Branchyata (2 species), Chelicerata (17 species) and Tracheata (more than 50 species).

The gradient of ecological factors along the catena exerts the major influence on spatial distribution of herpetobiotic arthropods. Their general abundance, es-

timated as dynamic density, is highest at the water margin (about 9000 ind.·m^{-2}·day^{-1}). Despite their different respiration mechanisms, both crustaceans and insects equally contribute to this huge activity.

Total dynamic density on the beach is 3.5 times less than at the water margin. The contribution of insects reaches 86%, the one of crustaceans decreases to 13.9%. Spiders are quite scarce.

Further up along the catena, the dynamic density of arthropods decreases by an order of magnitude, being nearly similar (190–220 ind.·m^{-2}·day^{-1}) on the cliff, abrasion plane and piedmont. Crustaceans contribute no more than 0.1%.The contribution of spiders, on the contrary, increases from 10% on the cliff to 22% on the abrasion plane. On the piedmontal plain their proportion reaches the maximum of 50% of all the animas caught.

Species richness

Species richness displays a pattern opposite to the one of dynamic density.

Water margin is characterised with the least number of arthropod species (9). On the beach species richness was 3 times as high, and remained at the same level further up along the catena.

Water margin, is inhabited by 2 species of crustaceans and 7 species of beetles. Beetles make the major contribution into species richness on the beach (17 species out of 26). Spiders and crustaceans are represented by 7 and 1 species, respectively. On the cliff beetles and spiders each account for *ca.*50% of the total number of species. Crustaceans are again represented by 1 species. This taxonomic structure is maintained further up along the catena (Fig. 2).

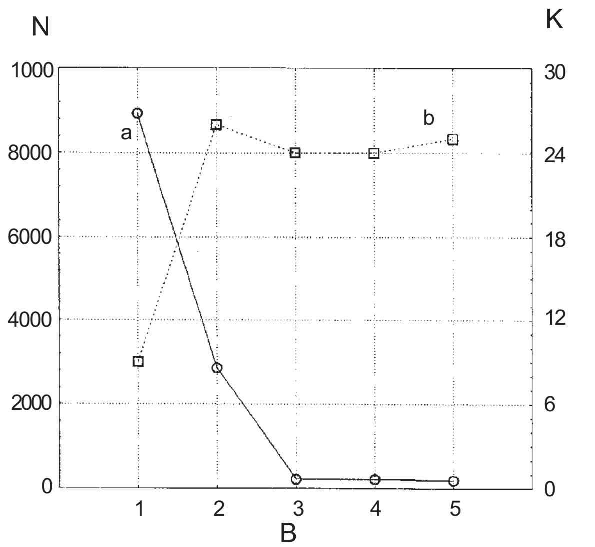


Fig. 2. Arthropod dynamic density (a) and species richness (b) on the Kunashir seashore catena: N — density, ind./m^{-2}/day^{-1}; K — number of species; B — biotopes.

Рис. 2. Динамика плотности популяции (a) и видовое богатство (b) на береговой катене острова Кунашир: N — плотность популяции, экз./м^2/сутки; K — число видов; B — биотопы.

Taxonomic composition

Similar levels of species richness on different catenary positions are maintained by different taxa of arthropods. At the water margin crustaceans are represented by 2 species: wood-lice *Ligia* sp. (Isopoda, Oniscoidea) and maritime flea *Orchestia ochotensis* (Crustacea, Amphipoda) (Table 1). Among the beetles Staphylinidae are represented by 4 species, and Histeridae by 2 species (Table 2). Species richness of all the above-mentioned taxa progressively decreases up along the catena.

Species number of Tenebrionids, represented by just 1 species on the water margin, significantly increases on the beach (6 species). In drier positions the black-beetle diversity drops again to the minimum.

Ground beetles (Carabidae), are absent at the water margin, and scarcely represented on the beach (2 species), not taking into consideration animals visiting occasionally (Table 2).

On the beach spiders are represented by 6 species (Table 3). Beginning from the cliff Tenebrionidae comprise the major part of arthropod species richness, increasing from 40% (cliff) to 60% (abrasion plane) and 70% (piedmont). The rest part is contributed by spiders and harvestmen. Wolf-spiders account for up to 70% of spider species. The contribution of spiders belonging to the Gnaphosidae, Thomisidae, Agelenidae families is less pronounced (Table 3).

Discussion

Ecological ordination of species

Changes of environmental conditions along the Catena provide a natural mechanism determining the distribution of species and the ecological ordination of arthropod species [Mordkovich et al., 1985; Mordkovich, Lyubechansky, 1998]. The catena position with the maximal population density is considered as preferential for a given species. Species with similar patterns of catenary distribution form one ecological group. The members of the group respond similarly to changes in at least the limiting environmental factor.

Despite the fact, that they are present in communities of other catenas studied [Mordkovich et al., 1985; Mordkovich, Lyubechansky, 1998], eurybionts are not found on the catena studied.

Based on the preference of a certain position, five ecological groups of species were distinguished, regardless of taxonomy.

The group of amphibionts is composed of certain crustaceans, insects and chelicerates adapted to the amphibiotic environment of the water margin. Crustaceans *Orchestra ochotensis* and *Lygia* sp. Reach very high densities. However, the distribution of *Lygia* is restricted by the littoral and beach sites, whereas maritime fleas penetrate (though at very low densities) the highest catena positions.

Among insects Staphylinidae, Histeridae, Tenebrionidae also join this ecological group. The prefer-

Table 1. Distribution of crustaceans along the seaside catena of the Kunashir Island (Ivanovsky foreland) (ind.·m^{-2}·day^{-1})
Таблица 1. Количественное распределение ракообразных (Brachiata) на приморской катене острова Кунашир (мыс Ивановский), экз./м^2/сутки

Arthropods	Positions on the catena				
	1	2	3	4	5
Amphipoda					
Orchestia ochotensis Dana, 1852	3126±107	201±17	17±2	9±0.8	3±0.001
Oniscoidea					
Ligia sp.	1183±93	203±12	—	—	—

Notes: 1 — water margin, 2 — beach, 3 — cliff, 4 — abrasion plane, 5 — piedmont; "— " — species absent.
Условные обозначения: 1 — урез воды, 2 — пляж, 3 — клиф, 4 — абразионная терраса, 5 — пьедмонт; "— " — вид отсутствует.

Table 2. Distribution of soil surface beetles (Coleoptera: Tenebrionidae, Staphylinidae, Histeridae, Carabidae) along the seaside catena of the Kunashir Island (Ivanovsky foreland) (ind.·m^{-2}·day^{-1})
Таблица 2. Количественное распределение напочвенных жуков (Coleoptera: Tenebrionidae, Staphylinidae, Histeridae, Carabidae) на приморской катене острова Кунашир (мыс Ивановский), экз./м^2/сутки

Arthropods	Position of the catena				
	1	2	3	4	5
Tenebrionidae					
Callicomus riederi (Fald., 1833)	2633±121	11±2	—	—	—
Gonocephalum coriaceum Motsch., 1857	—	—	15±0.9	—	—
G. recticolle Motsch., 1866	—	253±44	—	—	—
Idisia ornata Pascoe, 1866	—	544±61	—	—	—
Micropedinus algae Lewis, 1894	—	55±6	—	—	—
Phaleromella humeralis (Marsham, 1876)	—	966±74	—	—	—
Stenophanes mesostena Solsky, 1871	—	20±7	—	—	—
Staphylinidae					
Caphius nudus Scharp, 1874	896±32	—	—	—	—
Coprophillus impressus Scharp, 1889	20±3	4±1	—	—	—
Hadropinus fossor Scharp, 1889	933±71	5±0,3	—	—	—
Liusus hilleri Weise, 1877	30±0.8	7±0.5	—	—	—
Tachinus japonicus Scharp, 1888	—	—	3±0.2	—	—
Histeridae					
Hister concoice Lewis, 1884	?	?	?	?	?
Hypocaccus lewisi Schmidt, 1890	100±12	33±2	2±0.1	—	—
H. varians Schmidt, 1890	11±0,3	—	—	—	—
Carabidae					
Amara communis (Panzer, 1797)	—	2±0.06	27±4	2±0.1	—
A. fudjii Tanaka, 1959	—	—	—	—	2±0.3
A. tibialis (Paykull, 1798)	—	—	3±0.1	—	—
Badister lacertosus Sturm, 1815	—	—	6±0.9	11±2	—
B. marginellus H.Bates 1873	—	—	3±0.03	—	—
Bembidion quadriimpessum Motsch., 1860	—	30±6	—	—	—

Table 2 (continue)
Таблица 2 (продолжение)

Calathus micropterus (Duft., 1812)	—	—	—	2±0.5	36±3.2
Calosoma maximowiczi A.Mor., 1863	—	—	—	—	8±0.8
Carabus arboreus Lewis, 1882	—	—	—	—	6±0.2
C. arvensis hokkaidensis Lapouge, 1921	—	1±0.1	2±0.3	5±0.1	21±1.3
C. granulatus yezoensis H.Bates, 1883	—	—	—	4±1	—
C. kolbei Roeschke, 1897	—	—	—	—	7±0.6
C. kurilensis Lapouge, 1913	—	—	—	—	1±0.02
C. opaculus Putzeys, 1875	—	—	—	7±0.3	—
C. rugipenuis Motsch., 1861	—	1±0.02	3±0.3	4±0.6	11±0.9
Craspedonotus tibialis Schaum, 1863	—	5±0.4	—	—	—
Cychrus morawitzi Gehin, 1863	—	—	—	—	2±0.1
Dromius kurilensis Lafer, 1989	—	—	—	—	8±0.2
Epaphius ephippiatus H.Bates, 1873	—	—	—	—	18±2.8
Eucolpodes japonicum (Motsch., 1860)	—	—	—	—	2±0.1
Harpalus latus (L., 1758)	—	—	6±2	8±0.7	—
Leistus niger Gebler, 1847	—	—	—	4±1.1	17±1.8
Notiophilus Impressifrons A.Mor., 1862	—	—	—	—	1±0.01
Parena tripunctata (H.Bates, 1873)	—	—	—	—	1±0.01
Poecilus fortipes Chaudoir, 1850	—	—	15±2	8±1.5	—
P. reflexicollis (Gebler, 1830)	—	—	—	65±7	—
Pterostichus adstrictus Esch., 1823	—	—	—	—	6±0.3
P. haptoderoides (Tschit., 1888)	—	—	—	8±0.9	—
P. orientalis (Motsch., 1844)	—	—	—	3±0.5	—
P. rhaeticus Heer, 1838	—	—	—	—	2±0.01
P. ripensis Motsch., 1865	—	3±0.09	40±0.7	5±0.1	—
P. subovatus Motsch., 1862	—	1±0.01	3±0.2	—	—

Notes the same Table 1.
Условные обозначения те же, что в таблице 1.

ence of water margin is most expressed by the black beetles *Callicomus riederi* as well as staphylinids *Caphius undus* and *Hadropinus fossor*, and to a less extent by beetles *Coprophiphillus impressus, Liusus hilleri* and *Hypocaccus* (Table 2).

The common characteristics of representatives of this ecological group is that they belong to the most primitive clades of their respective tribes. For instance, the species *Callicomus riederi* belongs to the Phaleriini tribe, displaying the maximal species number of plesiomorphic features among the black beetles [Medvedev, 1977]. Rove beetles of the water margin belong to the Staphylinini tribe, the most ancient tribe in the family [Tikhomirova, 1979]. The same is true for the genus*Ligia* among Oniscoidea and*Orchestia* among Amphipoda.

All representatives of amphibiotic group possess a special physiological or behavioural mechanisms to tolerate abrupt changes in environmental conditions, caused by tide activity, e.g. rigid exoskeleton, flexible tergites, big subelytral bags, short elytra etc.)

The ecological group of beach hygrophiles consists mainly of black beetles (Tenebrionidae). Most of those are primitive forms of the main tribes of the family, which evolved mostly in dry landscapes(*Phaleromella humeralis* of Phaleriini*, Idisia ornata* of Idisini*, Micropedinus algae* of Pedinini, and *Gonocephalum recticolle* of Opatrini). Only *Stenophanes mesostena* represents the forest tribe of Mysolampini tribe. However, this species occupies a special niche under tree trunks deposited to the beach by storms. The highest had the populations of *Phaleromella humeralis*, *Idisia ornata* and *Gonocephalum recticolle* (Table 2). Mesophilic or hygrophilic beetle species, are poorly represented on the beach. Only *Bembidion quadriimpessum* is. These small beetles use actively soil

cracks which may explain their relatively low capture by the Barber's traps (Table 2). Also is *Craspedonotus tibialis,* surviving the intertidal sand heating due to the ability to store moist air in tracheas and cavities or to dig holes into the sandy substrate. Harvestmen, spiders *Drassodes lapidosus* and *Lycosa ishikariana* also contribute to the composition of this ecological group. During the hot period, harvestmen keep their body at 5–10 mm above the sand surface, and spiders hide themselves in crevices (Table 3).

All the species of the group have common hygrophilic preferences and ability to hide in soil during dry periods.

The ecological group of mesophiles, preferring cliff, consists mostly of ground beetles and spiders. Tenebrionids are represented only by *Gonocephalum coriaceum* (Table 2). Among carabids, *Pterostichus ripensis* are very typical, represented by smaller 40 ind.·m^{-2}·day^{-1}) and bigger (15 ind.·m^{-2}·day^{-1}). Spiders show weak preference for the cliff area. In contrast to the first two groups, mesophiles do not have pronounced adaptations to attend dryness or excessive moistening.

The ecological group of the meadow oligophiles, preferring the abrasion plane, is composed of ground beetles and spiders. The main representatives are *Poecilus reflexicollis*, *Badister lacertosus*, *Pterostichus haptoderoides* and wolf-spiders *Pardosa plumipes,* and *P. riparia.*

The ecological group of the forest oligophiles is comprised of animals preferring the forests of piedmont. Small ground beetles *Calathus micropterus, Leistus niger, Epaphius ophippiatus*, inhabiting forest litter, and big Carabini (*Carabus rugipenuis, C. arvensis, C. colbei, C. arboreus, Cychrus morawitzi, Calosoma maximowitzi*), roaming litter surface,

Table 3. Distribution of soil surface chelicerates (Chelicerata) along the seaside catena of the Kunashir Island (Ivanovsky foreland) (animals·m^{-2}·day^{-1})

Таблица 3. Количественное распределение напочвенных хелицеровых (Chelicerata) на приморской катене острова Кунашир (мыс Ивановский), экз./м^2/сутки

Arthropods	Positions on the catena				
	1	2	3	4	5
Opiliones					
Opiliones sp.	—	40±6	2±0.1	—	—
Aranei					
Gnaphosidae					
Drassodes lapidosus (Walckenaer, 1802)	—	11±1	—	—	—
D. pubescens (Thorell, 1856)	—	—	4±0.1	1±0.01	—
Drassylus pr. pusillus (C.L.Koch, 1833)	—	—	7±0.5	2±0.1	—
Lycosidae					
Lycosa ishikariana (S.Saito, 1934)	—	33±2	—	—	—
Pardosa lugubris (Walckenaer, 1802)	—	—	—	13±1.7	43±5.8
P. plumipes (Thorell, 1875)	—	3±0.1	5±0.4	17±2	9±0.5
P. riparia (C.L.Koch, 1847)	—	—	5±0.4	17±1.8	21±2.3
Tarentula sp.	—	3±0.5	—	—	—
T. pulverulenta (Clerck, 1758)	—	3±0.3	5±0.2	—	—
Trochosa sp.	—	—	5±0.3	2±0.2	—
T. terricola (Thorell, 1856)	—	3±0.2	8±0.3	—	—
Xerolycosa nemoralis (Westring, 1861)	—	—	2±0.02	1±0.01	—
Thomisidae					
Xysticus ephippiatus (Simon, 1880)	—	—	2±0.02	6±0.3	4±0.6
X. saganus (Bosenberg et Strand, 1906)	—	—	—	2±0.1	13±0.2
Agelinidae					
Agelena sp.	—	—	—	—	4±0.06

Notes the same Table 1.

Условные обозначения те же, что в таблице 1.

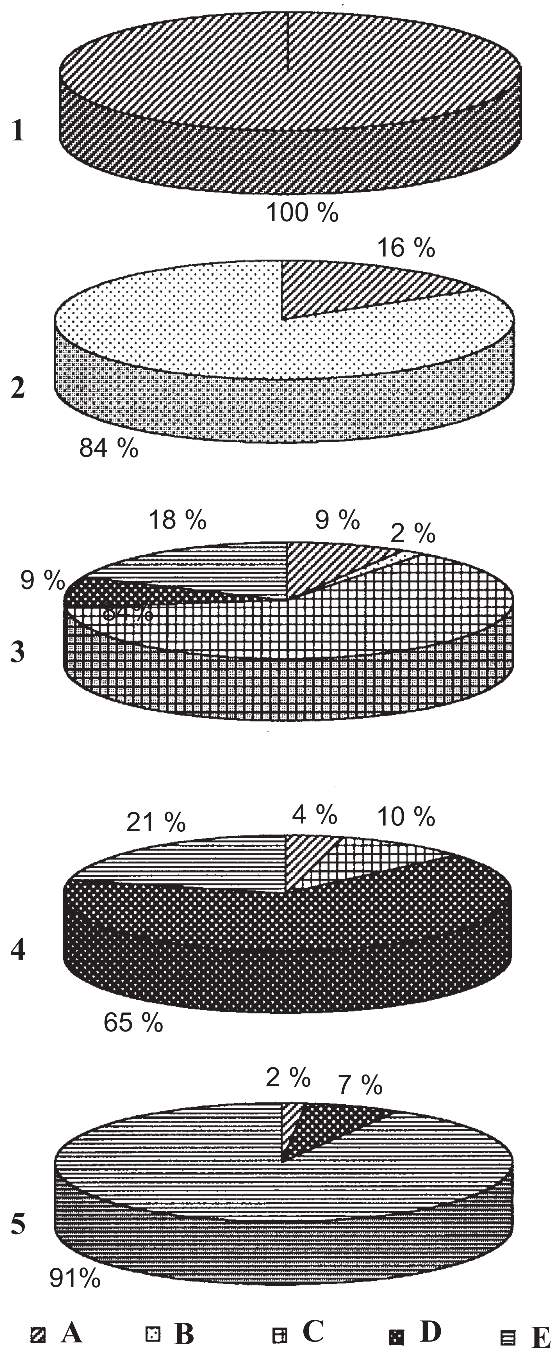


Fig. 3. Spectra of ecological groups of herpetobiotic arthropods on the Kunashir seashore catena (percent of the total number of individuals): amphibionts (A), beach hygrophiles (B), mesophiles (C), meadow oligiphiles (D), forest oligophiles (E). Catena positions are the same as on Fig. 1.

Рис. 3. Спектры экологических групп в сообществах герпетобионтных членистоногих на береговой катене острова Кунашир (%): амфибионты (A), береговые гигрофилы (B), мезофилы (C), луговые олигофилы (D), лесные олигофилы (E), позиции катены те же, что на рис. 1.

display the highest population density. Many representatives of the group have well-developed morphological adaptations to feed on molluscs. Crab-spiders *Xysticus saganus* and wolf-spiders *Pardosa lugibris* also contribute to this ecological group (Table 3).

Communities of herpetobionts

The density of populations and community composition change cleanly along the catena (Tables 1–3). As a result, different positions of the catena are occupied by different communities of herpetobionts (Fig. 3).

Along the seaside catena, where ecological conditions change rapidly and drastically, specific communities of arthropods develop on each of the geomorphologic positions.

The arthropod community of the water margin is composed of only 9 species with R-type life strategy [Grime, 1979]. The density of R-strategists the period of intensive seaweed decomposition may reach almost 10000 ind.$\cdot$m$^{-2}\cdot$day^{-1}. The index of Minkhinik is very low (0.1), indicating the ephemeral and primitive organisation of the community. All the species belong to the ecological group of amphibionts. Due to this fact this community differs drastically (0.9) from the community of the neighbouring catena position.

On the beach amphibionts account for only 17% of the arthropod population, the core of which is formed by the ecological group of beach hygrobionts (83%). Due to the increase in the 1) amount of represented ecological groups up to 5, 2) total number of species up to 24, and 3) total numbers of arthropods by 4–fold, Minkhinik's index increases up to 0.5. This value indicates the more balanced structure of the beach community, as compared to the one of the water margin. This functioning of the community is carried out by many members, rather than being limited to 1–2 species. The index of difference between beach and cliff communities is comparatively high, indicating a certain level of community separation.

The community of the cliff differs from the others in that it displays the maximal diversity of ecological groups. The key role is played by mesophiles (up to 63%); however, the contribution of other groups is also pronounced: meadow and forest oligophiles account for 8.5% and 18%, respectively, whereas amphibionts and beach hygrophiles account for 8 and 2%, respectively (Fig. 3). The Minkhinik's index of this community rises to 1.6, indicating its well-balanced structure and composition that is confirmed by stress-tolerant life strategy of the majority of species in the community [Grime, 1979]. Significant differences between the cliff community and those of the beach and abrasion plane (the indices are 0.8 and 0.6, respectively) indicate its specific character.

The community of the abrasion plane differs from the one on the cliff mainly in that another other ecological group of forest oligophiles is dominating (66%). The total number of ecological groups remains maximal (Fig. 3). Meadow oligophiles are highly specialised

inhabitants of soil surface, without any pronounced adaptations to digging or flying. According to the classification of Grime [1979], they are regarded as K-strategists (competitors). Resource (primarily food) deficit, forces them to occupy highly specialised ecological niches. It results in the decrease in population density and the rise in species diversity. That is why Minhinik's index still remains high (1.6). The difference between this community and the one on the cliff is less than the difference between this community and the one on piedmont (the index of difference is 0.8).

The piedmont community is comprised of species of only 2 ecological groups, with forest oligophiles as typical K-strategists accounting for more than 80% of the total numbers. Species diversity remains high, whereas abundance is moderate. Accordingly, the Minkhinik's index increases up to 1.8, and may be regarded as indicating the high community resistance to changing environmental conditions common on such a small ocean island as Kunashir. Over the whole catena the index of Mikhnik increases 18–fold.

Successions on the seashore

The spatial series of communities along the catena from the water to the watershed may be regarded as analogous to temporal succession. Successional changes in nature rarely happen within the limited area of a single habitat. Species substitution implies not only their elimination or emergence in a given habitat, but also immigration and emigration of species in the system of adjacent habitats. Along a catena succession processes take place simultaneously, though with different speed, in communities of all geomorphologic positions. The sequence of stages is similar everywhere, but the assortment and duration differ essentially [Mordkovich, 1988].

We believe that the sequence of ecological groups of species describe and explain succession better than species composition. In our study of the seaside catena the amphibiotic species mark zero , beach hygrophiles — pioneer, mesophiles — medial, meadow oligophiles — terminal and forest oligophiles — the climax stages of the development of the terrestrial community of herpertobionts of the Kunashir forests.

Several conceptual models ("stimulation", "tolerance" and "inhibition" have been developed to explain the mechanisms of succession [Connell, Slatyer, 1977].

According to the stimulation model, the organisms, which initiated succession, change their environment to the condition not suitable for themselves. However, their activity stimulates the flourishing of other groups and so forth until the initial resources are exhausted. At that point the community is forced back to its initial stage, and the succession starts again. It reminds the pendulum movement.

The model of tolerance implies that succession goes on until there are species able at least to tolerate the presence of other species, both of previous or subsequent stages of community development. Substitution of species is accompanied by the change in the dominant life strategy in the community and its development resembles a trend.

The model of inhibition reflects the situation when the presence of some species prevents the presence of others due to the high level of differentiation of ecological niches, including the chronological ones. Consequently, no unoccupied niches remain in the community [Odum, 1988]. As a result, the rate of successional changes slows down, and community development displays a cyclic pattern.

It is suggested that under different ecological conditions succession may follow one of the above models [Pickett et al., 1987]. However, on the seaside catena on the Kunashir island, communities at different geomorphologic positions follow different succession models; only at the middle position community development follows each model successively.

The simulation model is realised best on the water margin . Diurnal food tides prevent further community development and periodically bring it back to its initial condition.

On the beach periods of flooding alternate with periods of relative dryness of more prolonged duration than on the water margin. The combination of two ecological groups (amphibionts and beach hygrophiles) accounting together for 98% of the arthropod density, corresponds well to this environment. The dominance of beach hygrophiles indicates a more advanced stage of succession as well as the switch in successional model from stimulation to the tolerant one. That is confirmed by a substitution of ruderal (R) life strategy of amphibionts by the stress-tolerant (S) strategy of beach hygrophiles with increasing degree of dryness .The model of tolerance prevails in the community development. on the cliff which is seldom, only during severe storms, reached by waves and seaweed residues. During the interval between storms, amphibiotic species are substituted by beach hygrophiles, mesophiles, meadow and forest oligophiles.

The dominant role of meadow and forest oligophiles displaying K-strategy in abrasion plane and piedmont plane communities marks the climax and terminal stages of succession. Community follows the model of inhibition in its development. The substitution order of species and ecological groups is repeated from year to year. Any shifts may be noticed only in centennial dynamics.

Thus model of succession describe different stages of one and the same process of succession, rather than different types of successions.

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References

Anderssen J. 1985. Humidity responses and water balance of riparian species of Bembidiini (Col. Carabidae) // Entomol. Vol.10. No.4. P.363–375.

Berezina O.G., Mordkovich V.G. 2000. [Some experience in morphoecological classification of beetles (Insecta, Coleoptera)] // Siberian Ecol. Zh. No.3. P.271–277 [in Russian].

Connell J.H., Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization // Amer. Natur. No.982. P.1119–1144.

Evans W.G. 1977. Geografic variation, distribution and taxonomic status of the intertidial insect *T. barbarae* (Norn) (Col. Carabidae) // Quaest. entomol. Vol.13. No.2. P.83–90.

Ghilarov M.S. 1970. [Regularities in adaptations of arthropods to terrestrial life]. Moscow: Nauka Publ. 275 pp. [in Russian]

Grime J.P. 1979. Plant strategies and vegetation process. Chichester N.Y., Brisbane, Toronto: John Wiley and Sons. 212 pp.

King F.E., Fordy M.R., Elliott P.A. 1982. Comparison of the enviropropmental adaptations of the intertidal carabids*Aepus robini* (Labulbene) and *A. marinus* Strom // J. Natur. Hist. Vol.16. No.3. P.335–343.

Kryzhanovsky O.L., Okhotina M.V., Bromley G.F., Lafer G.Sh. 1975. [Review of ground beetles (Coleoptera, Carabidae) of the Kurils islands // [Entomological research on the Far East] / Trudy Biologo-Pochvennogo Inst. DVNTs AN SSSR, Vladivostok. Vol.23. No.131. P.119–142 [in Russian].

Krivolutskaya G.O. 1973. [Entomofauna of the Kurile islands]. Leningrad: Nauka Publ. 312 pp. [in Russian]

Magarran A.E. 1992. [Ecological diversity and its assessment]. Moscow: Mir Publ. 181 pp. [in Russian]

Mamkaev A.E. 1992. [Comparison of the morphological differences in lower and higher groups of the same phylogenetic trunk] // Zhurn. Obshch. Biol. Vol.29. No.1. P.48–56 [in Russian].

Medvedev G.S. 1977. [Taxonomic significance of the antenna sensillas of the black beetles (Col. Tenebrionidae)] // Trudy Vsesoyuznogo Entomol. Obshch. Leningrad: Nauka Publ. Vol.58. P.61–86 [in Russian].

Mordkovich V.G. 1988. [An assay on succession problems] // Trudy Sibirskogo Otd. AN SSSR, biol. ser. No.6/1. P.13–24 [in Russian].

Mordkovich V.G., Shatochina N.G., Titljanova A.A. 1985. [Steppe catenas]. Novosibirsk: Nauka Publ. 114 pp. [in Russian]

Mordkovich V.G., Lyubeshansky I.I. 1998. [Zonal-catenary order of the ecological ordination of the ground beetles population (Coleoptera, Carabidae) of the West Siberian plain] // Uspekhi sovremennoi biologii. No.2. P.205–215 [in Russian].

Odum U. 1986. [Ecology]. Moscow: Mir Publ. Vol.2. 376 pp. [in Russian]

Pickett S.T.A., Collins S.L., Armesto J.J. 1987. Models, mechanisms and pathways of succession // Botanical Review. Vol.3. P.335–371.

Ponomarenko A.G., Zherikhin V.V. 1980. Colepptera — zhestkokrylye // Istoricheskoe razvitie klassa nasekomykh [Historical development of insects] // Trudy Paleontol. Inst. AN SSSR. Moscow: Nauka Publ. P.75–84 [in Russian].

Smelyansky I.E. 1993. [Mechanisms of successions] // Uspekhi sovremennoi biologii. Vol.113. No.1. P.36–46 [in Russian].

Tshernyshev W.B. 1996. [Ecology of insects]. Moscow: Moscow University Publ. 297 pp. [in Russian]

Tikhomirova A.L. 1973. [Morphological and ecological peculiarities and phylogenesis of staphylinids]. Moscow: Nauka Publ. 191 pp. [in Russian]

Topp W. 1979. Insecten der Watten und Strande das “Hohen Knechtsandes” // Beitr. Naturkunde Niedersachs. Bd.32. H.4. S.106–112.

Torness J.B., Brundsen D. 1981. [Geomorphology and time]. Moscow: Nedra Publ. 226 pp. [in Russian]